

Observations on the Mechanism of Detecting Mucous Trail Polarity in the Snail *Littorina irrorata*

by

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Abstract. Marsh periwinkles, *Littorina irrorata*, can detect the polarity of conspecific mucous trails for at least 60 min after they are deposited. Experiments indicate that trail polarity detection does not involve discriminating a longitudinal concentration macro-gradient of a volatile chemical substance using the paired cephalic tentacles. If only one cue provides trail polarity information, then a bilateral trail asymmetry, a topography-based physical map, and a reflected light pattern are probably not involved either. The possibility that trail polarity information is obtained from directional microstructures in gastropod mucous trails is discussed.

INTRODUCTION

CRAWLING GASTROPOD MOLLUSKS typically deposit a mucous trail on the substratum, and this trail may subsequently be detected by a predator or conspecific. Many early studies of conspecific trail following by gastropods were surveyed by COOK & COOK (1975), COOK (1977), and HAMILTON (1977a). More recent studies have documented conspecific trail following in *Ilyanassa obsoleta* (TROTT & DIMOCK, 1978), *Achatina fulica* (CHASE *et al.*, 1978), *Onchidium verruculatum* (MCFARLANE, 1980), *Mariella dussumieri* (USHADEVI & KRISHNAMOORTHY, 1980), *Nerita textilis* (CHELAZZI *et al.*, 1985), and other *Littorina* species (GILLY & SWENSON, 1978; RAFTERY, 1983).

Many of these gastropods exhibit a preference for following their own or a conspecific's mucous trail in a specific direction. In *Biomphalaria*, *Ilyanassa*, *Littorina*, and *Physa*, the trail is followed preferentially in the same direction in which the trail-depositing snail was traveling; we refer to this response as following the trail "with polarity." In *Onchidium*, *Nerita*, and *Siphonaria*, the trail is followed preferentially in the opposite direction, or "against polarity." In either case, directional trail following probably involves a two-stage response: recognition of the presence of a conspecific mucous trail, followed by determi-

nation of trail polarity. Each stage could involve different stimuli and sensory mechanisms.

Contact with a mucous trail by cephalic or anterior tentacles appears necessary for detecting the presence of a trail in *Littorina planaxis* (PETERS, 1964) and some other gastropods. The tentacles are required to detect the polarity of a trail in *L. irrorata* (Robbins & Hamilton, in preparation). The exact mechanism involved in trail polarity detection has not been determined for any gastropod, although the following mechanisms have been suggested:

Concentration macro-gradient mechanism—involves sampling a longitudinal concentration gradient of some volatile chemical substance in the trail, at the points where the two anterior tentacles contact the trail (usually 6 to 10 mm apart). This mechanism requires use of the two tentacles, and it assumes that the snail's approach path is approximately perpendicular to the trail when contact is made.

Concentration micro-gradient mechanism—involves sampling a similar longitudinal concentration gradient, but along a distance equivalent to the width of one tentacle tip (usually less than 1 mm). According to this mechanism, only one tentacle would be required to detect trail polarity. Using both tentacles would merely furnish duplicative information.

Physical map mechanism—involves detecting some physical feature of the trail across an area in the plane

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of the trail. The feature could be a repetitive pattern of topography (ridges and troughs in the surface of the mucus) or of viscosity (thin and thick mucus). Only one tentacle would be required for this mechanism, but the tentacle would have to contact a large enough area of the trail to discern the physical pattern. This mechanism was suggested by the mucous trails of *Littorina* and some other gastropods, which show repetitive patterns when stained (see Figure 2).

Bilateral asymmetry mechanism—involves the two sides of the trail having different chemical or physical properties (e.g., substance A in left side and substance B in right side), and the existence of some simple decision rule for determining trail polarity (e.g., turn left if A is detected first when a trail is contacted, but turn right if B is detected first). This mechanism would require only one tentacle. This mechanism was suggested by the fact that the foot of *Littorina*, and other gastropods that locomote by ditaxic pedal waves, exhibits bilateral organization in structure and neuromotor control.

Reflected light mechanism—involves determining trail polarity visually, by optical effects of mucus on light reflected from the trail. This mechanism was suggested by the fact that some gastropods can orient relative to light patterns reflected from the substratum (CHARLES, 1961).

Directional microstructure mechanism—involves detecting microstructures in the trail which are morphologically or chemically polarized. This mechanism would require only one tentacle.

GILLY & SWENSON (1978) hypothesized that a concentration macro-gradient mechanism is involved in trail following by *Littorina sitkana* and *L. littorea*. RAFTERY (1983) concluded that a concentration macro-gradient mechanism was likely for *Littorina* and that, if a structure-based mechanism was involved, the structural units providing polarity information must be smaller than 35 μm .

We have studied trail following in *Littorina irrorata* Say, a common inhabitant of marshes along the northern Gulf of Mexico. Snails rest on plant stems during high tide, but once the tide recedes they usually descend to the sand-mud substratum, where they crawl about and feed. When encountering conspecific mucous trails on the substratum, snails often follow these trails with polarity (HALL, 1973; HAMILTON, 1977b). RUSSELL (1980) found that those *L. irrorata* following mucous trails in laboratory arenas followed them with polarity 92.2% of the time ($n = 421$).

Our primary objective was to determine whether *Littorina irrorata* uses a concentration macro-gradient mechanism to detect the polarity of conspecific mucous trails. Experiments were conducted using a Y-maze enclosed within a controlled-stimulus environment. In addition, several other hypothesized mechanisms of polarity detection were examined, the effect of trail age on the ability to detect trail polarity was evaluated, and some general features of trail following behavior and mucous trail organization were described.

GENERAL METHODS

Adult *Littorina irrorata* (shell length >15 mm; shell width >11 mm) were collected from marshes bordering on Santa Rosa Sound, Escambia County, Florida. Snails were housed in plastic containers under simulated natural lighting conditions, and were used within 3 days after collection. General observations were made in shallow pans. All observations and experiments were conducted with the snails in air, the medium in which they are normally active.

Polarity detection tests were conducted in a Y-maze constructed of white plexiglas (Figure 1). A 3-cm length of mucous trail, specially modified in most experiments, was positioned near the junction and oriented perpendicular to the approach path of a test snail. The 4-cm wide path cut in the plastic base was restricted to a 2-cm wide path by overhanging strips of plastic bonded to the base (Figure 1B). This design forced snails approaching the junction to follow a fairly straight path while preventing them from climbing up the side of the maze. Three pieces of flat-black paper (9 cm high) were attached vertically at the ends of the maze opposite from the approach path of a test snail. One piece of paper (9 cm wide) was oriented perpendicular to the approach path of a test snail; the other two pieces (4 cm wide) were positioned at the ends of the left and right forks of the maze. The black pieces of paper ensured that test snails oriented first toward the maze junction, and then along one of the two forks. (The visual responses of *Littorina irrorata* are described by HAMILTON & WINTER [1982].)

Two identical mazes were constructed and used, and subsequent data analysis showed no significant differences between mazes. To eliminate any effect of possible left or right turning preferences on the data, tests were organized so that the same choice required left turns and right turns to be made equally often.

Straight lengths of mucous trail for testing were obtained using a 5-mm thick wooden base in which was cut a straight, 12-cm long channel designed with overhangs similar to those of the Y-maze. A piece of black paper (12 \times 9 cm) was attached vertically at one end of the channel in order to better orient the trail-depositing snail. The mucous trails were deposited on either glass plates or disposable clear plastic strips (0.1 mm thick) positioned beneath the channel.

During polarity detection tests, the Y-maze was placed inside a special arena having homogeneous white walls and a diffuse overhead light source. Light intensity on the arena floor was 2800 lux for all experiments, except for Experiment 7, which was run in darkness. A mirror beneath the arena floor permitted observation of a snail's progress during a test. For further details of arena structure see HAMILTON & WINTER (1982).

Certain response criteria were used in all experiments. Any snail not moving within 3 min after placement in the Y-maze, or taking longer than 10 min to enter one arm of the maze after initial movement, was discarded and

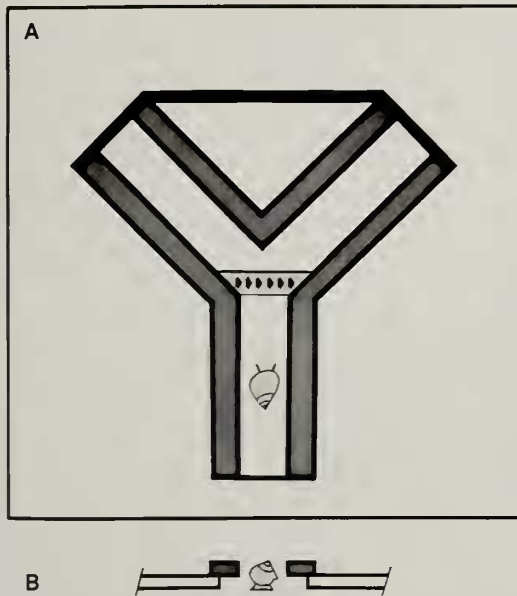


Figure 1

A. Top view of Y-maze used to study trail polarity detection. Three black paper targets (thickest lines) were 9 cm high. The maze was placed on the surface bearing the test mucous trail (stippled) so that the trail was positioned at the end of the approach path. The trail is drawn wider than normal. The arrows indicate the direction in which the trail-depositing snail was traveling. A mucous trail's width is normally about 50% of the depositing snail's shell width. A test snail is shown halfway along the approach path. B. Cross-sectional view of test snail on approach path showing overhangs (shaded). All tests with the maze were conducted in a special arena.

never used again. Also, we ignored the response of any snail not traveling up the center of the approach arm of the maze. Each snail's actual path was determined by direct observation from beneath during a test, and by examination of the test snail's mucous trail by misting (HAMILTON, 1977a) after the test. These precautions, and the narrow width of the approach arm of the maze, ensured that each cephalic tentacle of a test snail sampled a different section of those mucous trails that had been cut transversely and manipulated; this was especially important in Experiments 3 and 4. A snail had to move at least 2 cm into either fork of the maze to have made a choice. The choice of fork was assumed to have been influenced by trail polarity cues, even if the test snail did not follow the trail along its full available length, as was often the case. Each snail was tested only once.

RESULTS

General Observations

Figure 2 shows a *Littorina irrorata* mucous trail deposited on a white enamel surface and subsequently stained with 1% methylene blue for 2 min. The difference in stain



Figure 2

Stained mucous trail of *Littorina irrorata* showing chevron-shaped pattern of zones of high stain uptake. The 1-cm long arrow indicates the direction in which the trail-depositing snail was traveling.

pattern between left and right halves of the trail reflects the ditaxic pedal waves characteristic of littorinid locomotion. Chevron-shaped zones of high stain uptake are located at regular intervals; these zones appear to be produced by the front edge of each half of the foot as each half proceeds forward incrementally. Observations with the light microscope revealed a complex arrangement of microfibrils within the trail. Fibers have been reported in the mucous trails of *Ariolimax* (DENNY & GOSLINE, 1980), *Helix* (SIMKISS & WILBUR, 1977), and *Ilyanassa* (BRETZ & DIMOCK, 1983).

When a *Littorina irrorata* is crawling over a surface, the tip of each cephalic tentacle is brought into contact with the surface about once every 3 s. In an adult, contact points on the surface are spaced about 8 mm apart. As a tentacle tip is lifted, it is often dragged toward the snail a short distance (less than 1 mm) before "popping free" from its adhesive bond with the surface. Many snails begin turning with polarity only a few seconds after the tentacles make their first contact with the edge of a trail.

Experiment 1: Polarity Detection

This experiment was conducted to determine the normal frequency of trail polarity detection in the test apparatus. Test mucous trails were deposited on glass plates.

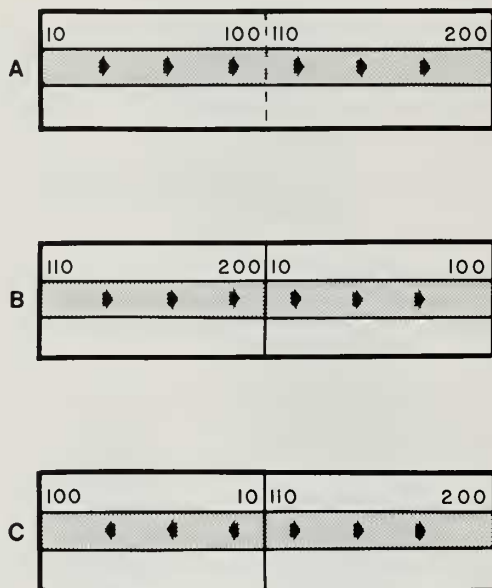


Figure 3

A. Length of mucous trail on long plastic strip. Numbers indicate approximate times (in s) when different sections of the trail were deposited. Dashed line shows where plastic and trail were cut after trail deposition. B. Manipulation of trail for Experiment 3. Assumed concentration gradient was made artificially high at the center, but the actual trail polarity was unchanged. C. Manipulation of trail for Experiment 4. Assumed concentration gradient was made artificially high at the center, while other potential cues were rendered directionally ambiguous. Arrows as in Figure 1.

Of 40 snails tested, 34 (85%) turned with polarity and 6 turned against polarity ($\chi^2 = 19.6$, $P < 0.001$). We conclude that *Littorina irrorata* shows a significant tendency to follow mucous trails with polarity in the experimental apparatus.

Experiment 2: Time Study

A 5- to 10-min interval normally occurred between deposition of a test mucous trail and actual testing of that trail. This experiment was designed to ensure that the polarity information provided by the trail did not change significantly over even longer periods. Test mucous trails were deposited on plastic strips which were then air dried for either 30 or 60 min before testing. Of 20 snails tested for each time interval, 18 snails turned with polarity and 2 turned against polarity ($\chi^2 = 12.8$, $P < 0.001$, for each time interval). The data show that *Littorina irrorata* mucous trails retain polarity information after at least 60 min of air exposure.

Experiment 3: Concentration Macro-gradient Mechanism—I

We tested the concentration macro-gradient hypothesis in two experiments. The first experiment was designed to

determine whether snails could detect correct trail polarity when the assumed concentration macro-gradient was artificially reversed at the point on the test trail where a test snail first made contact with it. Each test mucous trail was deposited on a plastic strip. For illustration purposes here, approximate time values are assigned to four points on the trail. The oldest end of the trail was designated $T = 10$ s, and the most recently deposited end was designated $T = 200$ s (see Figure 3A). The plastic strip was then cut transversely between the $T = 100$ and $T = 110$ s points on the trail, thus producing two sections of mucous trail on plastic. The positions of both sections of mucous trail were then switched, thereby connecting the $T = 10$ s part of the trail to the $T = 200$ s part of the trail. The actual direction in which the mucous trail was deposited thus remained the same for each section (see Figure 3B). The manipulated trail was then positioned in the Y-maze so that the test snail first contacted the trail at the junction of the two sections, and hence had the opportunity to sample both sections of trail. As mentioned above, pre- and post-test observations ensured that test snails actually sampled both sections of trail.

If a test snail turned toward the most recently deposited part of the trail ($T = 200$ s), it would turn against polarity; alternately, if a test snail turned toward the oldest part of the trail ($T = 10$ s), it would turn with polarity. Of 20 snails tested, 18 turned with polarity and 2 turned against polarity ($\chi^2 = 12.8$, $P < 0.001$). Thus, these data suggest that trail polarity detection does not depend primarily on a concentration macro-gradient mechanism.

Experiment 4: Concentration Macro-gradient Mechanism—II

This experiment was designed to determine whether snails could detect an assumed concentration macro-gradient when other potential cues about trail polarity were rendered directionally ambiguous. Test mucous trails were deposited on plastic and cut into two sections, as in the previous experiment. However, for this experiment, the oldest section of trail (time values from $T = 10$ to $T = 100$ s) was rotated 180° (see Figure 3C).

In this situation, if a concentration macro-gradient could be detected, most snails would be expected to turn right; alternatively, if a concentration macro-gradient could not be detected, an equal number of snails would be expected to turn left as right. Of 20 snails tested, 11 turned left and 9 turned right ($\chi^2 = 0.01$, $P > 0.25$). Thus, these data suggest that a concentration macro-gradient of a volatile chemical substance is not involved in trail polarity detection by *Littorina irrorata*.

Experiment 5: Physical Map Mechanism—Topography

As mentioned above, when a *Littorina* mucous trail is stained with methylene blue, chevron-shaped zones appear where more stain is taken up than by immediately surrounding areas (Figure 2). We considered the possi-

bility that the darkly stained zones might contain a deeper layer of mucus than in surrounding areas, and that the entire trail might have a regular pattern of topographic relief in the form of alternating ridges and troughs. This experiment was designed to learn if snails could still detect trail polarity after the trail was compressed so as to reduce or eliminate any assumed topographic relief.

Test mucous trails were deposited on glass plates. Each trail was compressed by applying finger pressure evenly against a plastic strip placed over the trail. A few mucous trails treated in this fashion still revealed a faint chevron pattern when stained, but most did not. Each glass plate bearing a compressed trail was tested in the Y-maze in the arena. Of 20 snails tested with compressed trails, 19 turned with polarity and 1 turned against polarity ($\chi^2 = 16.2$, $P < 0.0005$). These data suggest that a physical map in the form of a topographic relief pattern is not required for trail polarity detection.

Experiment 6: Bilateral Asymmetry Mechanism

The plastic strips used for compressing mucous trails (Experiment 5) hardly ever revealed the chevron pattern when stained, but imprints of the mucous trails were clearly visible on them. The left and right edges of these trail imprints coincided with the right and left edges of the original trails. This experiment was designed to learn if trail polarity detection requires a bilateral trail asymmetry coupled with a simple decision rule.

The plastic strips produced in Experiment 5 were placed at the junction of the Y-maze in the arena. If the trail edges were physically or chemically different, and a simple decision rule were involved, then snails tested with the trail imprints should have turned against polarity. Of 20 snails tested with these trail imprints, 18 turned with polarity and 2 turned against polarity ($\chi^2 = 12.8$, $P < 0.005$). Thus, this result suggests that a bilateral trail asymmetry, coupled with a simple decision rule, is not required for trail polarity detection. Retention of a stainable chevron pattern is apparently not critical either.

Experiment 7: Reflected Light Mechanism

As *Littorina irrorata* can see quite well (HAMILTON & WINTER, 1982; HAMILTON *et al.*, 1983), this experiment was conducted to test the possibility that reflected light patterns might reveal trail macrostructure, and hence trail polarity. Test mucous trails were deposited on glass plates. The arena lights were off during this experiment. The measured light intensity on the arena floor was less than 1 lux, which is below the threshold intensity required for *L. irrorata* to orient significantly toward a 5°-wide vertical black bar (HAMILTON & WINTER, 1982). Test snails were reluctant to run the Y-maze in such darkness, so two changes in protocol were effected to stimulate their movement. First, the arena slope was adjusted so that the approach path ran 5° upslope toward the junction. *Littorina irrorata* can detect slopes this small (Hamilton, unpublished data). Second, each *L. irrorata* was permitted to

wipe its cephalic tentacles on the mucus of a *Melongena corona* for 30 s before release in the maze. *Littorina irrorata* orient upslope at almost twice their normal speed after contact with a *Melongena*, their natural gastropod predator (Hamilton, unpublished data).

Of the 20 snails that ran the maze, 17 turned with polarity and 3 turned against polarity ($\chi^2 = 9.6$, $P < 0.005$). These data indicate that *Littorina irrorata* can detect trail polarity using other than visual cues.

DISCUSSION

A *Littorina irrorata* contacting a conspecific mucous trail with its cephalic tentacles usually turns with polarity almost immediately, and proceeds along the trail. The most commonly proposed hypothesis for the mechanism enabling this rapid determination of trail polarity has been a concentration macro-gradient involving some volatile chemical substance.

Three pieces of evidence argue against a concentration macro-gradient mechanism being involved in polarity detection in *Littorina irrorata*. First, although polarity information appears to last less than 30 min in the trails of some gastropods, this information lasts for at least 60 min (the longest time that we tested) in *L. irrorata* (Experiment 2); furthermore, Russell (unpublished data) found that *L. irrorata* showed a significant ability to detect polarity in trails dried in air for 24 to 36 h before testing. (A trail's presence could be detected for more than 72 h.) If a single volatile chemical substance were involved, such long-lasting trail polarity information would require a slow evaporation rate and, in turn, an incredibly low difference discrimination threshold for the snail's chemosensory system. A chemical macro-gradient involving several substances, each with a different evaporation rate, might be more easily detected over a long period. Second, snails tested with a manipulated trail ignored an artificially high (and assumed) concentration gradient in favor of some other cue or cues (Experiment 3). GILLY & SWENSON (1978) obtained the same result in a similar experiment (their "point of paradox test") with *L. littorea*. And third, snails showed no directional preference when encountering a manipulated trail having an artificially high (and assumed) concentration gradient, but being directionally ambiguous otherwise (Experiment 4).

Our experiments indicated that several other mechanisms were not required for polarity detection to occur. A physical map depending on topographic cues (Experiment 5) and retention of a stainable chevron pattern (Experiment 6) are probably not required for trail polarity detection. These findings were expected because simple observation reveals that snails often begin turning with polarity after the cephalic tentacle tips make a single contact with the edge of a trail. After contacting the substratum, a tentacle tip is dragged a distance of less than 1 mm before "popping free" from the substratum, and the entire trail is 5 to 7 mm wide in adults; sampling $\frac{1}{2}$ of a trail's width is probably insufficient to determine its gross physical features (*e.g.*, chevron curvature). Also, tests with trail

imprints showed that polarity detection does not require bilateral asymmetry cues. Finally, snails tested in light levels below the threshold for detecting a large high-contrast target still followed trails with polarity (Experiment 7). Therefore, trail polarity detection apparently does not require reflected light cues.

These experiments suggest that detection of a concentration macro-gradient of a volatile chemical substance is not *involved* in trail polarity detection, and that detection of a bilateral trail asymmetry, a reflected light pattern, or a gross topographic pattern are not *required* for trail polarity detection. The distinction in terminology and conclusion is important. Interpretation of data from animal orientation experiments must be made with recognition that many species possess redundant sensory systems and orientational strategies, arranged in a hierarchy of dependence (ABLE, 1980). For example, just because snails can still detect trail polarity in darkness, one should not conclude that trail polarity cannot be detected from reflected light patterns under lighted conditions; snails may possess several methods of detecting trail polarity, and even depend *primarily* on reflected light patterns during the day, but they may simply use an alternative method when tested in darkness. Failure to recognize this point is probably responsible for many of the ambiguous conclusions obtained in some studies of homing mechanisms in mollusks.

We could not determine if a viscosity-based physical map mechanism is involved in trail polarity detection. However, we consider it unlikely that a repetitive viscosity pattern is necessary for trail polarity detection because, again, snails often begin turning with polarity after only a single contact with just the trail edge. The concentration micro-gradient hypothesis was not examined either. However, the concentration difference in a gradient would be greater over a distance of 8 mm (the distance between the points where the tentacle tips contact the substratum) than over a distance of 1 mm (the width of a tentacle tip). So, because *Littorina irrorata* seem unable to use a concentration macro-gradient to detect trail polarity, it seems unlikely that the more difficult micro-gradient mechanism would be involved.

If one is willing to risk assuming that redundant trail polarity cues are not involved here, and that a viscosity-based physical map and a concentration micro-gradient are not involved, then one is left with the directional microstructure mechanism. In the mucous trails (and pedal glands) of *Helix*, a terrestrial pulmonate, SIMKISS & WILBUR (1977:fig. 12) found many 4.5- μ m long rodlets. The rodlets were all frayed at one end and pointed at the other end, and were all oriented with their unfrayed end pointing in the direction in which the trail-depositing snail had been traveling. How such small structures become arranged in such an orderly fashion is unknown. We have found no reports that *Helix* follows mucous trails. *Ilyanassa* does detect trail polarity; BRETZ & DIMOCK (1983) reported seeing occasional frayed or split filaments in the trail and, after treating trails in various ways, they con-

cluded that the structural integrity of the mucous trail is important for trail following.

We have found no equally detailed studies of mucous trail microstructure for other gastropods, so it is not known whether other species possess similar polarized structures in their trails. COLE *et al.* (1977) described what is apparently a morphologically unique bacterium from various tissues in an aquatic snail; in its cephalotrichous form, this bacterium looks very similar to the frayed rodlets described for *Helix*. It is interesting that both the frayed rodlets in *Helix* trails, and the cephalotrichous bacteria, fit easily within RAFTERY's (1983) 35- μ m size criterion for the possibility that the trail polarity cue in *Littorina* might be structural, rather than chemical. Information on trail microstructure and pedal gland morphology for species from different taxonomic groups and ecological settings would be useful for comparison.

Whatever mechanism for trail polarity detection is eventually shown to be involved in trail following by *Littorina irrorata*, there is no reason to believe that the same mechanism is involved in other gastropods. Mucus is chemically and structurally complex (GRENON & WALKER, 1980; BOUSFIELD *et al.*, 1981), and there are probably several ways of including polarity information in it. *Littorina irrorata* is behaviorally terrestrial, and its trail retains polarity information for a much longer period than the trail of some other gastropods. Species active when submerged in water may use a very different mechanism than *L. irrorata*.

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